J. New York Entomol. Soc. 104(1–2):62–69, 1996

MORPHOLOGICAL CASTE DIFFERENCES IN NEOTROPICAL SWARM-FOUNDING POLISTINAE WASPS. V—*PROTOPOLYBIA EXIGUA EXIGUA* (HYMENOPTERA: VESPIDAE)

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Abstract.—A slight dimorphism between queens and, workers and intermediates was found in a colony of *Protopolybia exigua exigua* collected in Pedregulho, southeastern Brazil. Mean sizes of all nine measured body parts of queens (n = 30) were statistically larger than those of workers and intermediates. Canonical discriminant analysis also showed some differentiation among them, with Mahalanobis' intercaste distance (D^2) 4.95 between queens and workers, 5.63 between queens and intermediates and 1.84 between intermediates and workers.

Key words: Vespidae; Polistinae; *Protopolybia exigua exigua*; caste differences; multivariate analysis.

Among many fascinating aspects underlying colonial organization in social insects, caste related problems are surely outstanding. On such matters the most impressive aspect involves the diversity of caste patterns that, in turn, suggests the plasticity of evolutionary strategies leading to them. Neotropical swarm-founding Polistinae, in which polygyny is a rule, have remained less explored, mainly due to the difficulty of studying them continuously under both experimental and natural conditions. On the other hand, to some extent reliable sociological and biological information about these wasps can be obtained by analyzing a sample of wasps taken from a particular nest. This is especially true for caste differentiation and related phenomena.

Caste differentiation in Polistinae is not pronounced (Richards, 1978). However, the Epiponini tribe has been morphometrically analyzed and, as pointed out by Richards (1971, 1978; Richards and Richards, 1951), at least three caste differentiation stages are found: 1-Conspicuous size and allometric differences present, with queens larger than workers in the absence of intermediates (sense Richards and Richards, 1951) (*Agelaia* spp: *A. areata,* Jeanne and Fagen, 1974; *A. pallipes* and *A. multipicta,* Simões et al., in prep.; *A. vicina,* Noll et al., in prep.; *Protonectarina sylveirae,* Shima et al., 1996b); 2-Conspicuous dimorphism present, with queens smaller than workers and no intermediates present (*Apoica flavissima,* Shima et al., 1994; *Polybia dimidiata,* Maule-Rodrigues and Santos, 1974; Shima et al., 1996a); 3-Morphological differences slight or indistinct, and intermediates present (*Pseudopolybia vespiceps,* Shima et al., in prep.). Evidently this group remains biometrically very little explored. Most of the relevant papers (e.g. Richards and Richards, 1951; Richards, 1971, 1978) aimed primarily at caste distinction for taxonomical purposes, and so only characteristics supposedly more reliable for such aims were emphasized.

The employment of a standardized methodology, as in multivariate analysis, has supported the establishment of patterns for the comparison of caste differentiation among the epiponine. Morphometric analysis on a *Protopolybia exigua exigua* colony are reported here showing that queens are slightly larger than workers and intermediates.

MATERIAL AND METHODS

The whole population, consisting of workers, intermediates and queens, was taken from a young colony of *Protopolybia exigua exigua* (de Saussure) collected in Pedregulho (Southeastern Brazil) on Feb. 2, 1995. In order to detect morphological differences between castes the whole population was measured under a binocular microscope. The measured body parts were: head width (HW), minimum interorbital distance (IDm), gena width (GW), width of mesoscutum (MSW), alitrunk length (AL), length of gastral tergum I (T_1L), basal height of T_1(T_1BH), basal width of tergum II (T_2BW), and partial length of the forewing (distance between the anterior edge of the first submarginal cell and the final margin of the marginal cell) (WL). The numerical data were statistically analyzed in relation to the ovarian and spermathecal states. The statistical analysis including the canonical discriminant analysis (CDA: Rao, 1973) were performed with the SAS Program Package for PC computers, and Kruskal-Wallis One Way analysis of variance on ranks was used in order to detect caste differences for each character. If differences were detected, Dunn's method for multiple comparison was performed using the program Sigma Stat for Windows version 1.0.

RESULTS

Nests and related aspects: *P. exigua exigua* occurs from NW South America (Colombia, Bolivia) to Southern Brazil (Richards, 1978) and, according to him: "the nests consist of a comb suspend from a leaf or branch by one or more peduncles and surrounded by an envelope in the side or bottom of which is an exit-hole; the envelope is attached to the sides of the combs. When there are additional combs they are built on the envelope of the previous one with a new envelope and exit hole. Generally, only one comb is found but one additional one is not rare."

The one-combed analysed nest (Fig. 1) had 307 cells in which 46 contained only eggs indicating the precocious state of the nest. It was attached by one principal peduncle and two auxiliaries ones. Concerning population size it was counted at 28 workers, 37 intermediates and 30 queens.

Ovarian development and insemination: In the analyzed sample three kinds of ovary development were recognized (Fig. 2): type A, developed ovarioles bearing from two to several mature oocytes, type B, ovarioles with some oocytes at the begining of development and/or some in final phase of vitelogenesis and, type C, filamentous ovarioles bearing from no visible to slightly developed oocytes. Since only in the A type females the spermatheca contained sperm, females with ovaries A, B and C can be characterized as queens, intermediates and workers, respectively. As a probable consequence of the colony's early stage, differences in the ovary condition between queens and intermediates were not clear and, in some cases, only insemination distinguished queens and intermediates.

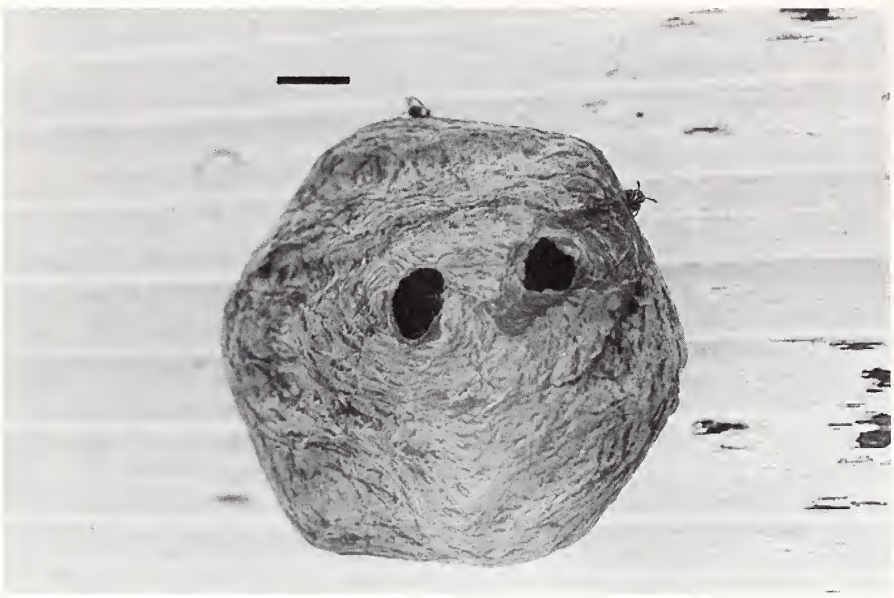

Fig. 1. Nest of *Protopolybia exigua exigua.* (Scale bar = 1.0cm).

Caste differences in relation to morphometry: Among the mean relationships of the 9 analysed characters (Table 1), all of them show the comparisons between queen-worker and queen-intermediate significantly different. In contrast, intermediate-worker comparisons were not significantly different ($p < 0.05$).

The result of the canonical discriminant analysis based on 9 morphological char-

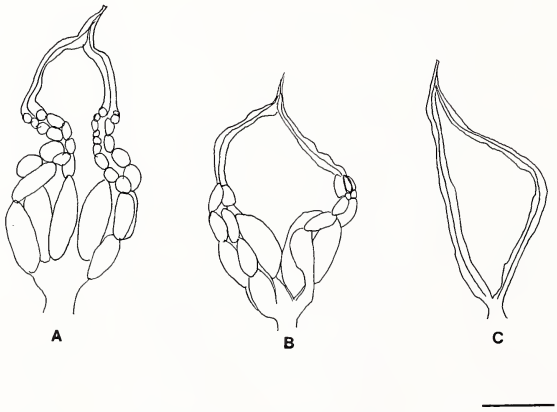

Fig. 2. Kinds of ovary development found among the females of *Protopolybia exigua exigua.* A, developed ovaries found in inseminated females; B, developed ovaries found in uninseminated females (intermediates) and C, undeveloped ovaries found in uninseminated females (workers). (Scale bar = 1.0mm).

Table 1. Means, CAN_1 and CAN_2 values and observed values of Dunn's test for 9 characters used for discriminating castes of *Protopolybia exigua exigua*.

Characters	*Means (mm)*			*Dunn's Method (Difference on Ranks)*			CAN_1		CAN_2	
	Queens (n = 32)	*Workers* (n = 34)	*Interme-diates* (n = 40)	*Q/W*	*Q/I*	*I/W*	*Raw*	*Stand-ardized*	*Raw*	*Stand-ardized*
Head										
HW	3.54 ± 0.04	3.49 ± 0.06	3.49 ± 0.03	23.7*	30.8*	7.00	0.68	0.03	−10.71	0.55
IDm	2.20 ± 0.05	2.13 ± 0.08	2.15 ± 0.05	18.6*	26.0*	7.44	−3.35	−0.23	8.63	0.58
GW	0.60 ± 0.04	0.56 ± 0.05	0.57 ± 0.03	19.9*	22.8*	2.91	1.02	0.04	−2.37	−0.10
Mesosoma										
MSW	2.57 ± 0.07	2.50 ± 0.07	2.48 ± 0.06	24.1*	30.3*	6.22	4.45	0.33	−2.59	−0.19
AL	2.76 ± 0.06	2.65 ± 0.11	2.63 ± 0.06	30.8*	35.5*	4.63	0.02	0.002	−1.26	−0.12
Metasoma										
T_1L	2.59 ± 0.06	2.46 ± 0.10	2.44 ± 0.11	34.9*	40.7*	5.81	5.71	0.65	−3.13	−0.36
T_1BH	0.55 ± 0.03	0.48 ± 0.05	0.48 ± 0.03	37.0*	38.2*	1.24	16.67	0.80	5.63	0.27
T_2BW	1.65 ± 0.05	1.58 ± 0.09	1.55 ± 0.06	25.1*	36.1*	11.0	−0.14	−0.01	−7.31	−0.59
Wing										
WL	4.56 ± 0.07	4.41 ± 0.13	4.45 ± 0.10	29.3*	38.0*	8.68	0.50	0.06	10.36	1.22

* statistically significant

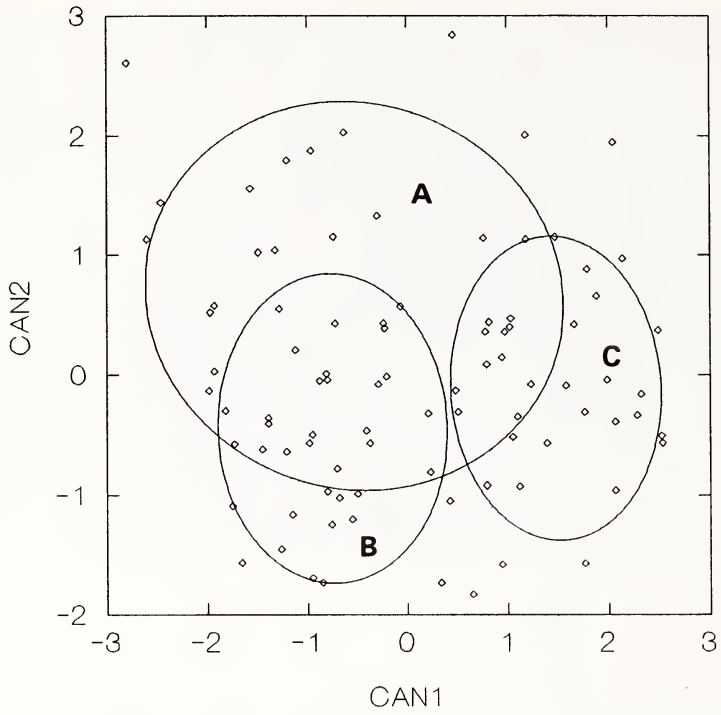

Fig. 3. Discrimination among intermediates (A), workers (B) and queens (C) of *Protopolybia exigua exigua* based on the canonical discriminant analysis using 9 metric characters. Each ellipse encompasses 67% of the variation found in each group.

acters suggests slight dimorphism between queens and, workers and intermediates. Queens showed higher values of the first canonical variable (CAN_1) than workers and intermediates (−0.36 to 3.44 vs. −2.8 to 2.12 and −3.0 to 1.0, respectively) (Fig. 3). On the other hand, intermediates showed higher values of the second canonical variable (−1.80 to 3.00), than queens (−1.80 to 2.20) and workers (−4.20 to 1.00). According to Figure 3 queens are different but slightly from workers and intermediates.

To calculate CAN_1 and CAN_2 the following equations were used:

$$CAN_1 = 0.68(HW - 3.50) - 3.35(IDm - 2.16) + 1.02(GW - 0.58) + 4.45(MSW - 2.51) + 0.02(AL - 2.68) + 5.71(T_1L - 2.49) + 16.67(T_1BH - 0.50) - 0.14(T_2BW - 1.59) + 0.50(WL - 4.48)$$

$$CAN_2 = -10.71(HW - 3.50) + 8.63(IDm - 2.16) - 2.37(GW - 0.58) - 2.59(MSW - 2.51) - 1.26(AL - 2.68) - 3.13(T_1L - 2.49) - 5.63(T_1BH - 0.50) - 7.31(T_2BW - 1.59) + 10.36(WL - 4.48)$$

Table 2. Classification results for group comparisons through discriminant analysis in *Protopolybia exigua exigua.* (Other explanations in the text).

	Predicted Group frequency (percentage)			
Actual group	Workers	Intermediates	Queens	Total
Workers	12 (42.86)	8 (28.57)	8 (28.57)	28 (100.00)
Intermediates	12 (32.43)	23 (62.16)	2 (5.41)	37 (100.00)
Queens	1 (3.33)	0 (0.00)	29 (96.67)	30 (100.00)

For determining CAN_1 (Table 1), minimum interorbital distance (IDm), width of mesoscutum (MSW), length of gastral tergum I (T_1L), and, especially, basal height of T_1 (T_1BH), were the most important among the characters examined and in CAN_2, head width (HW), minimum interorbital distance (IDm), basal width of tergum II (T_2BW), and, especially, wing length (WL) were the most important among the characters examined. The Mahalanobis distances (D^2: Anderson, 1968) calculated through the CDA were 4.95 between queens and workers, 5.63 between queens and intermediates and, 1.84 between intermediates and workers. These values indicate slight separation between inseminated (queens) and uninseminated (workers and intermediates) females. At the same time, workers and intermediates were not significantly differentiated, as suggested above.

Comparing actual groups with predicted groups through discriminant analysis (Table 2) it is evident that, although the values of Mahalanobis distances are low, queens form together a distinct group (96.67%) while workers and intermediates are scattered among the three predicted groups, but intermediates are more distinct (62.16%) than workers (42.86%).

DISCUSSION

Protopolybia exigua exigua presents slight caste differentiation between queens and uninseminated females (workers and intermediates), at least in the early stages of nest development, as compared to other taxa, for example *Agelaia* spp (*A. flavipennis,* Evans and West-Eberhard, 1970; *A. areata,* Jeanne and Fagen, 1974; *A. pallipes* and *A. multipicta,* Simões et al., in prep.; *A. vicina,* Noll et al., in prep.) that have well-developed caste differentiation and intermediates absent. Notwithstanding, group comparisons (Table 2) showed queens as the unique well defined group and intermediates and workers less differentiated. In addition, workers and intermediates are also slightly separated by CAN_2, values what suggest that these two groups are not well-defined and the intermediates could be a workers' ovary-development phase as suggested by Simões (1977).

The role of the intermediates remains largely unknown (Richards, 1978). Recent studies have provided some new insights about them. There are direct observations on their frequent egg-laying and oophagy in *Protopolybia exigua* (Simões, 1977) and *P. acutiscutis* (Naumann, 1970). Presently, ongoing morphological studies on caste differences have been providing interesting results on their distribution, morphological and physiological identities, etc. Intermediates were detected in *Protopolybia acutiscutis* (cited as *P. pumila* by Naumann, 1970), *P. pumila* (Letizio-

Machado, 1972), *P. exigua exigua* (Letizio-Machado, 1974: Simões, 1977), *Brachygastra lecheguana* (Letizio-Machado et al., 1988) and *B. scutellaris* (Carpenter and Ross, 1984); which have quite distinct morphological castes. In addition, intermediates are equally frequent in groups with caste scarcely evident on morphological grounds only (Richards and Richards, 1951; Richards, 1978).

Caste differences in Epiponini can be ordered into three main groups (see introduction). Compared to other taxa that have been studied *P. exigua exigua* has slight caste-differentiation and presents intermediates comparable to *Pseudopolybia vespiceps* (Shima et al., in prep.). However, different from *P. vespiceps, P. exigua* has queens more distinct from workers and intermediates (in *P. vespiceps* intermediates are more distinct), which is comparable to *Protonectarina sylveirae* (Shima et al., 1996b) and higher Mahalanobis distances (1.51, 1.12 and 0.99 for queens-intermediates, intermediates-workers and queens-workers, respectively, for *P. vespiceps.*) suggesting that *P. exigua* shows a more clear-cut caste differentiation than *P. vespiceps.*

ACKNOWLEDGMENTS

The authors acknowledge the financial support by Fapesp (Fundação de Amparo à Pesquisa do Estado de São Paulo) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) and James M. Carpenter (American Museum of Natural History) for his reading through the typescript and helpful suggestions.

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Received 11 June 1996; accepted 11 September 1996.